Effects of solar UV radiation on photosynthesis of the marine angiosperm *Posidonia oceanica* from southern Spain

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ABSTRACT: The effects of solar irradiance on the photosynthesis of the marine angiosperm *Posidonia oceanica* L. Delile were investigated by means of pulse amplitude-modulated (PAM) fluorescence in the Natural Park of Cabo de Gata-Níjar, southern Spain. The study was conducted in 2 different seasons, summer (September 1996) and winter (February 1997). Daily variation in the effective quantum yield ($\Delta F/F_\mathrm{m}'$) was determined in plants growing at 2.5 m and in plants transferred from 15 m to 0.5 and 2.5 m depth. Three different experimental designs were conducted: (1) Incubation of shoots under 3 different solar radiation treatments using cut-off UV filters: full solar radiation (PAR + UV-A + UV-B), solar radiation without UV-B (PAR + UV-A) and solar radiation without UV (PAR); (2) short-term exposure (30 min) to high solar irradiance (photoinhibitory phase) under all treatments followed by transfer fo the plants to low irradiance for 4 h (recovery phase); (3) Preincubation of plants for 4 d under the 3 cited treatments followed by short-term exposure (30 min) to high solar irradiance under PAR + UV-A + UV-B, PAR + UV-A and PAR. A significant decrease in $\Delta F/F_\mathrm{m}'$ occurred from dawn to noon (18 % in September and only 6 % in February), followed by total recovery during the afternoon in both seasons. The highest decrease in $\Delta F/F_\mathrm{m}'$ occurred in shoots illuminated with PAR + UV-A radiation. This decrease was more pronounced in winter than in summer, and was substantially higher in plants transferred from deep (15 m) to shallow water than in plants harvested at 2.5 m. Moreover, the recovery in the afternoon was higher in plants incubated at 2.5 m than in those transferred from 15 m to shallow waters. In the second set of experiments, short exposure (30 min) of plants collected from 2.5 m confirmed that inhibition under PAR + UV-A was higher than under PAR + UV-A + UV-B. In general, full recovery after exposure to high solar irradiance (PAR + UVA + UV-B) occurred only in PAR-treated plants in September. Finally, when shoots of *P. oceanica* were preincubated for 4 d under PAR, PAR + UV-A or PAR + UV-A + UV-B and then submitted to full solar irradiance at the water surface, the greatest reduction in $\Delta F/F_\mathrm{m}'$ was seen in plants grown under PAR, while the lowest occurred in PAR + UV-A + UV-B pretreated plants in both seasons. Recovery was higher in PAR + UV-A + UV-B pretreated plants. UV solar irradiance also affected both maximal electron transport rate (ETR) and the initial slope of the ETR-irradiance curves. *P. oceanica* seems to be well acclimated to high solar irradiance, showing a high capacity for recovery. Solar UV-B might be involved in the impairment and recovery of photosynthesis, since removal of UV-B promoted higher inhibition by solar irradiance. The absence of UV under high PAR for several days resulted in a partial loss of the capacity for photoprotection. We conclude that UV radiation could act in the natural habitat as a trigger for the induction of photoprotective mechanisms against high solar irradiance. The ecological implication of the beneficial role of UV-B in well-acclimated marine plants to high irradiance is discussed.

KEY WORDS: Marine angiosperms · PAM-fluorometry · *Posidonia oceanica* · UV radiation

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INTRODUCTION

Seagrasses contribute significantly to the productivity of coastal areas in both temperate and tropical waters (Phillips & McRoy 1980). In particular, the production of the endemic Mediterranean species *Posidonia oceanica* (L.) Delile has been well studied (Boudouresque et al. 1989). *P. oceanica* and its leaf epiphytes play a major role in the benthic primary production of the Mediterranean Sea (Pergent et al. 1994). Maximal photosynthetic capacity of this species is in the same range as that of the most productive macroalgae (Enríquez et al. 1995), and it makes a substantial contribution to the organic supply to neritic waters (Alcoverro et al. 1995).

Thinning of the ozone layer is resulting in increased levels of ultraviolet B (UV-B) radiation at the Earth's surface (Booth et al. 1994). Consequently, at present there is a considerable concern about the possible impact that increasing UV radiation (UVR) may have on natural ecosystems, especially marine systems (Smith et al. 1992, Franklin & Forster 1997). The evaluation of the effect of UV-B on marine macrophyte photosynthesis is crucial for evaluating the flow of carbon in the ocean in the scenario of global climate change (Häder & Worrest 1991). Seagrasses and benthic macroalgae are static and restricted to their site of growth, thus have no opportunity to avoid high irradiances of photosynthetically active radiation (PAR, λ = 400 to 700 nm) or UVR by vertical migration, unlike phyto-

plankton. This suggests that sublittoral seagrasses may show a lower tolerance to environmental stress, particularly to high irradiances and to UVR, while eulittoral plants should be more adapted to coping with higher UV levels at the surface. Recent studies have described a higher reduction of photosynthetic capacity in subtidal algae than in intertidal algae when exposed to full sunlight (Maegawa et al. 1993, Hanelt et al. 1997, Häder et al. 1998, Hanelt 1998). This reduction in photosynthetic capacity is followed by a decrease in growth rate, increasing pigment photobleaching and tissue damage in some brown and red macroalgae, from shaded and deep areas, after exposure to the sun (Wood 1987, Häder & Figueroa 1997).

Although many studies have focused on the ecophysiology of *Posidonia oceanica*, until recently there has been limited information on the effects of UVR on seagrasses in general (Trocine et al. 1981, Dawson & Dennison 1996, Beer & Björk 2000). *P. oceanica* grows preferentially in very clear waters with high penetration of photosynthetically active radiation (PAR) and of UVR; thus, we would expect this species to have efficient photoprotection mechanisms against excessive solar irradiance, as has been previously reported for intertidal macroalgae (Hanelt 1996, Figueroa et al. 1997, Flores-Moya et al. 1998).

In this work, the photosynthetic capacity of *Posidonia oceanica* was estimated by means of the pulse amplitude-modulated (PAM) fluorescence technique, which has been previously used in studies of terrestrial vascular plants and of seaweeds (Büchel & Wilhelm 1993, Franklin & Forster 1997, Häder & Figueroa 1997), and recently also in some seagrasses (Ralph & Burchett 1995, Dawson & Dennison 1996, Beer et al. 1998, Ralph et al. 1998, Beer & Björk 2000). Seasonal and short-term effects of solar irradiance (with and without UVR) on photosynthesis of *P. oceanica* in the natural environment, determined as changes in the effective quantum yield by means of PAM fluorometry, are discussed.

MATERIALS AND METHODS

Underwater light field. Underwater PAR and UVR were measured throughout the day by means of a profiling UV radiometer (Biospherical Instruments, Model PUV 500), while surface UVR was monitored every 2 min with a PUV 510A radiometer. The PUV 500 determines downwelling irradiance at 4 UV bands: 305 ± 1, 320 ± 2 nm, 340 ± 2 nm and 380 ± 2 nm, together with PAR by means of a broadband PAR sensor (400 to 700 nm).
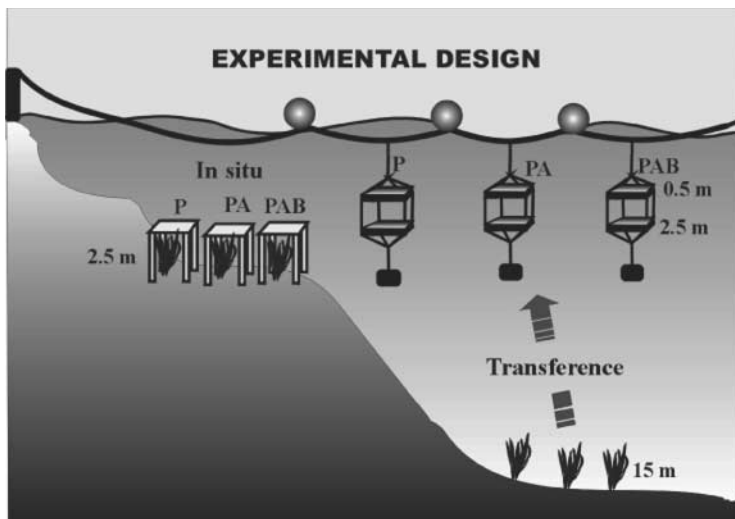

Fig. 1. Design of the different experiments conducted in September 1996 and February 1997 in waters of 'Playazo de Rodalquilar' (Cabo de Gata, southern Spain). *Posidonia oceanica* from 15 m were transferred to boxes with different cut-off filters suspended from surface buoys at depths of 0.5 and 2.5 m. Additional plants growing at a depth of 2.5 m were screened with different UV-cut-off filters. P: PAR; PA: PAR + UV-A; PAB: PAR + UV-A + UV-B

The PUV 500 system is equipped with a pressure sensor (depth) and a Sea Tech transmissometer (25 cm pathlength). This latter instrument allows determination of light transmission at each depth. The transmissometer was provided with a FFE-3100 LED source with peak wavelength at 660 nm and spectral line width of 40 nm. The beam attenuation coefficient (c), expressed in m^{-1}, provides a good estimation of the concentration of particulated material (Kirk 1994), and was calculated according to the equation:

$$c = (\ln T)/\delta x \qquad (1)$$

where T is the transmission and δx is the pathlength of the transmissometer (0.25 m).

The vertical attenuation coefficient of the downward radiation (K_d) was calculated in the PAR region and in the 4 UV bands by linear regression between the surface (0.1 m depth) and the different profiling depths according to the following equation:

$$K_d = (\ln E_0 - \ln E_z)/z \qquad (2)$$

where E_0 is the irradiance at the surface (0.1 m depth) and E_z the irradiance at the depth z.

In order to calculate the daily integrated irradiance (E_z) of PAR and UVR at different depths (z), the following expression was used:

$$E_z = E_0 e^{-(K_d z)} \qquad (3)$$

where E_0 was the daily integrated irradiance at the surface ($kJ\ m^{-2}$) and K_d the attenuation coefficient of the downward radiation.

UVR for the broad bands 280 to 320 (UV-B) and 320 to 400 nm (UV-A) was calculated from the irradiance values at 305, 320, 340 and 380 nm, applying the algorithms of Orce & Helbling (1997):

UV-B $= 59.5\ E_{305} + 4.1\ E_{320}$ ($r^2 = 0.997$, n = 320)
UV-A $= 87.4\ E_{340} - 2.4\ E_{380}$ ($r^2 = 0.998$, n = 320) (4)

Photosynthesis. The experiments were conducted in September 1996 and February 1997 on *Posidonia oceanica* (L.) Delile at El Playazo of Rodalquilar (Natural Park of Cabo de Gata-Níjar, Almería, southern Spain: 36° 52′ N, 2° 12′ W). This sublittoral species shows a seasonal growth pattern with a strong increase from February onwards, with a maximum in spring. In summer, active growth stops until the next spring (Ott 1980). Fig. 1 summarizes the experimental design used.

In situ exposure experiments: External and healthy shoots of *Posidonia oceanica* were collected at 2.5 m (subtidal plants). They were then placed on the sea bottom and covered *in situ* with different UV cut-off filters placed 20 cm above the plants (Fig. 1). The light treatments used were: (1) full solar irradiance (PAR + UV-A + UV-B); (2) solar irradiance without UV-B (PAR + UV-A), and (3) solar irradiance without UVR (PAR). The PAR irradiance was obtained by interposing Ultraphan filters (Digefra GmbH, Munich, Germany) with transmission at λ > 395 nm, and will be called Treatment 'P' throughout this paper. In order to cut off only UV-B radiation, Folex filters (Folex GmbH, Dreieich, Germany) with transmission at λ > 320 nm were used; this light treatment, whereby the plants received PAR + UV-A will be named 'PA'. The filters absorbed 10% of the incident radiation; thus an Ultraphan filter 295 (with transmission at λ > 295) was used for the PAR + UV-A + UV-B treatment to achieve the same irradiance among treatments; this will be referred to as Treatment 'PAB'. The spectral characteristics of these filters have already been described by Figueroa et al. (1997).

The decay of the effective quantum yield ($\Delta F/F_m'$) during the day was determined with the PAM fluorometer (see next subsection). The experiments were started 1 d after deployment of the selective filters, and external leaves of *Posidonia oceanica* were collected every 2 to 3 h, from sunrise to sunset, after 2 and 4 d under the different light treatments.

Transference experiments: *Posidonia oceanica* shoots, consisting of rhizomes with several fascicles of leaves, were collected at 15 m depth and introduced into custom-made UV-transparent boxes, covered with the cut-off filters described above, and suspended from surface buoys at 0.5 and 2.5 m (Fig. 1). The shoots were transplanted from their growth site to the experimental area in black plastic bags. Daily cycles of ($\Delta F/F_m'$) were conducted after 2 and 4 d of incubation.

Exposure and recovery experiments: Samples of *Posidonia oceanica* freshly collected from 2.5 m depth were submitted to short-term exposure (30 min) under full solar irradiance in surface waters (0.05 m depth) under different Schott UV-cut-off filters (transmission at λ < 295, < 320 and < 400 nm), and the fluorescence was measured after light treatment and at different times after placing the samples in the shade (recovery period). These experiments were also conducted with *P. oceanica* shoots previously grown for 4 d under P, PA and PAB treatments at 2.5 m depth.

Fluorometry. The fluorescence parameters were estimated immediately after harvesting by means of a PAM fluorometer (PAM 2000, Waltz) according to Schreiber et al. (1986). The effective quantum yield was calculated as $\Delta F/F_m'$, where $\Delta F = F_m' - F_t$ (F_t = the current steady-state fluorescence, Genty et al. 1989; F_m' = maximal fluorescence of light-adapted plants). The plants were harvested by SCUBA divers and transported to a site where measurements were carried out within 15 min under previously standardised dim-light conditions (ca. 50 μmol m^{-2} s^{-1}). During this 15 min period no recovery of the effective quantum yield and no significant differences (Tukey′s test, p <

0.05) from the effective quantum yields of the plants in its growth site were observed (Viñegla 2000).

In order to simplify the presentation of the results, the percentage of inhibition and recovery of effective quantum yield are expressed as:

$$\% \text{ decrease in } \Delta F/F_m' = [(\Delta F/F_m'_{(morning)} - \Delta F/F_m'_{(noon)})/ (\Delta F/F_m'_{(noon)})] \times 100 \quad (5)$$

$$\% \text{ recovery of } \Delta F/F_m' = [(\Delta F/F_m'_{(afternoon)} - \Delta F/F_m'_{(morning)})/ (\Delta F/F_m'_{(morning)})] \times 100$$

these being the morning values measured around dawn (08:00 to 08:30 h, local time), the noon values at 14:00 h in September and at 13:00 h in February, and the afternoon values around dusk (18:30 to 19:30 h).

Quantum yield under actinic irradiance, supplied by the red-light diode (LED) of the PAM-2000 fluorometer, was estimated in samples of *Posidonia oceanica* collected in the late afternoon (after a daily cycle). The shoots were exposed to increasing irradiance of between 0 and 650 µmol m^{-2} s^{-1} at incubation intervals of 30 s, according to Hanelt (1998). The electron transport rate (ETR) was calculated by multiplying the effective quantum yield ($\Delta F/F_m'$) by the incident irradiance of PAR (E_{PAR}), the absorptance (A) of the samples and a factor of 0.5, because it is assumed that 4 of the

8 electrons necessary to assimilate 1 CO_2 molecule come from Photosystem II (PSII) (Schreiber et al. 1986):

$$\text{ETR} = \Delta F/F_m' \times E_{PAR} \times A \times 0.5 \quad (6)$$

Absorptance (*A*) was calculated from the optical density (OD) value determined in a spectrophotometer (Beckman DU-7) using an opal glass according to Shibata (1957), as follows:

$$A = 1 - 10^{-OD} \quad (7)$$

The average absorptance for the samples collected in February 1997 was 0.85, and for those collected in September 1996 it was 0.75.

Fitting of the ETR versus irradiance curves was performed by modifying the non-linear function of Jassby & Platt (1976), including a term of photoinhibition according to Platt et al. (1980), as follows:

$$\text{ETR} = [\text{ETR}_{max} \times \tanh ((\text{ETR}_{is} \times E)/\text{ETR}_{max})] \times e^{(-\beta \times E/\text{ETR}_{max})} \quad (8)$$

where ETR is the electron transport rate, ETR_{max} is the saturated ETR, tanh is the hyperbolic tangent function, ETR_{is} is the efficiency of the electron transport (initial slope of the ETR vs irradiance curves), *E* is the incident irradiance, and β is the slope of the inhibitory phase. The saturation irradiance for the electron transport (E_k) was calculated as the intercept between the ETR_{max} and ETR_{is} values, and the inhibition irradiance (E_{inh}) as the intercept between ETR_{max} and the exponential inhibitory phase.

Statistical analysis. Data were compared by means of a 2-way (time of day and solar radiation conditions) Model I ANOVA. Tukey's HSD test was applied when significant differences were found among treatments. In all cases, normality of data was assessed by the Kolmogorov-Smirnov test and homogeneity of variance was verified by the Barlett's test when the number of replications was n ≥ 6 or the F_{max} test in the case of n ≤ 5 replications. All the statistical tests were carried out in accordance with Sokal & Rohlf (1995).

RESULTS

Underwater light field

Penetration of both PAR and UVR was very high in Cabo de Gata during the experimental period, as expected for very clear coastal waters (Fig. 2) (Type I in Jerlov's classification). The vertical attenuation coefficient decreased from shorter wavelengths (e.g. 305 nm) to longer ones (e.g. 320, 380 nm) and PAR (Fig. 2). The spectral composition of underwater irradiance was enriched in blue-green wavelengths
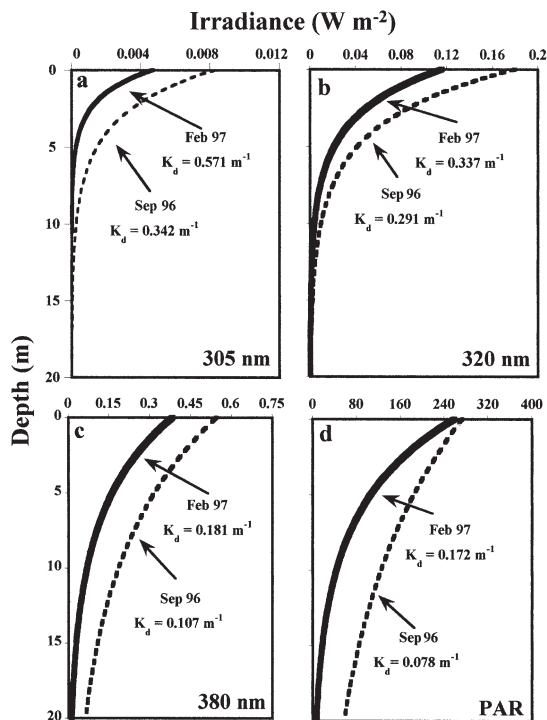

Fig. 2. Vertical profiles of different wavebands of UVR: 305, 320 and 380 nm and PAR (400 to 700 nm) in the waters of Cabo de Gata in September 1996 and February 1997. Attenuation coefficient values (K_d) for each waveband are indicated
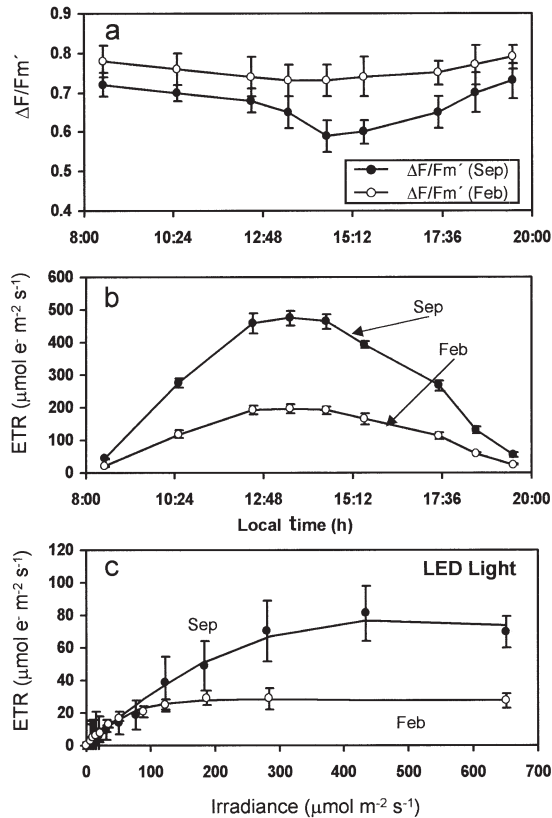
Fig. 3. *Posidonia oceanica.* Daily variations in (a) effective quantum yield ($\Delta F/F_m'$) and (b) electron transport rate (ETR) in plants collected from 2.5 m depth in September 1996 and February 1997; (c) ETR versus irradiance, determined by applying the LED light from the PAM 2000 during incubation periods. Each curve represents the mean of 4 replicates

reached ~22 m in September and 11 m in February (Table 1).

The weekly integrated irradiance of PAR and UVR was calculated at the different depths at which the experiments were conducted, i.e. 0.5, 2.5 and 15 m (Table 1). The surface weekly integrated irradiance was ~1.6 times higher in September than in February for PAR, 2.3 for UV-A and 5.4 for UV-B. The ratio UVR/PAR was 1.5 times higher in summer than in winter, resulting in higher the UV signals.

Daily cycles of effective quantum yield and electron transport rate (ETR)

The effective quantum yield in *Posidonia oceanica* growing at 2.5 m depth decreased from morning to noon, recovering in the afternoon (Fig. 3a). The decrease in $\Delta F/F_m'$ at noon was significantly higher (Tukey's test, $p < 0.01$) in September (18%) than in February (6%), and full recovery occurred in the after-

Table 1. Attenuation coefficient of downward radiation (K_d in m^{-1}) for PAR (400 to 700 nm), UV-A (320 to 400 nm) and UV-B (280 to 320 nm); water transmission (T); beam attenuation coefficient (c); depth at which 1% of surface irradiance is reached (h) for PAR, UV-A and UV-B; and weekly dose at the water surface and at the different depths in which the experiments were conducted (0.5, 2.5 and 15 m) in September 1996 and February 1997

Variable	18–25 Sep 96	8–15 Feb 97
K_d (PAR) (m^{-1})	0.078 ± 0.008	0.172 ± 0.044
(UV-A) (m^{-1})	0.154 ± 0.080	0.318 ± 0.020
(UV-B) (m^{-1})	0.210 ± 0.011	0.404 ± 0.039
T (%)	84.750 ± 2.185	80.160 ± 0.298
c (m^{-1})	0.780 ± 0.060	0.890 ± 0.070
h (PAR) (m)	59.040 ± 4.210	25.440 ± 2.546
(UV-A) (m)	29.900 ± 2.345	14.480 ± 1.387
(UV-B) (m)	21.930 ± 2.657	11.399 ± 0.950
Weekly dose (kJ m^{-2})		
Surface		
PAR	60578.82	38128.39
UV-A	9612.36	4215.20
UV-B	259.91	48.09
0.5 m		
PAR	58260.90	31346.38
UV-A	8899.00	3236.00
UV-B	233.90	35.36
2.5 m		
PAR	49840.00	21825.93
UV-A	6540.00	1713.16
UV-B	153.70	15.76
15 m		
PAR	18801.66	2524.40
UV-A	954.13	35.74
UV-B	11.14	0.11

(data not shown), as expected for very clear coastal waters (Kirk 1994). The attenuation coefficient (K_d) of UV-B radiation was higher than that of UV-A radiation (Table 1). On the other hand, the K_d of PAR was ~2.3 to 2.7 and ~1.8 to 2.0 times lower than that of UV-B and UV-A respectively (Table 1). Higher attenuation coefficients at all wavebands were observed in winter. This is due to a lower transmission and consequently a higher beam-attenuation coefficient in winter than in summer because of the increased presence of particles in winter. In summer, the beam-attenuation coefficient (c) was 13% higher in winter than in summer; however, the light penetration was 100% higher in summer than in winter (Table 1). The concentration of particles, estimated from beam-attenuation values, was 1.7 ± 0.1 mg l^{-1} in February and 1.3 ± 0.1 mg l^{-1} in September.

Thus, 1% surface PAR irradiance penetrated to 59 m in September and ~25 m in February (Table 1) while 1% of UV-A irradiance penetrated to ca. 30 m in September and 14 m in February. Finally, 1% UV-B
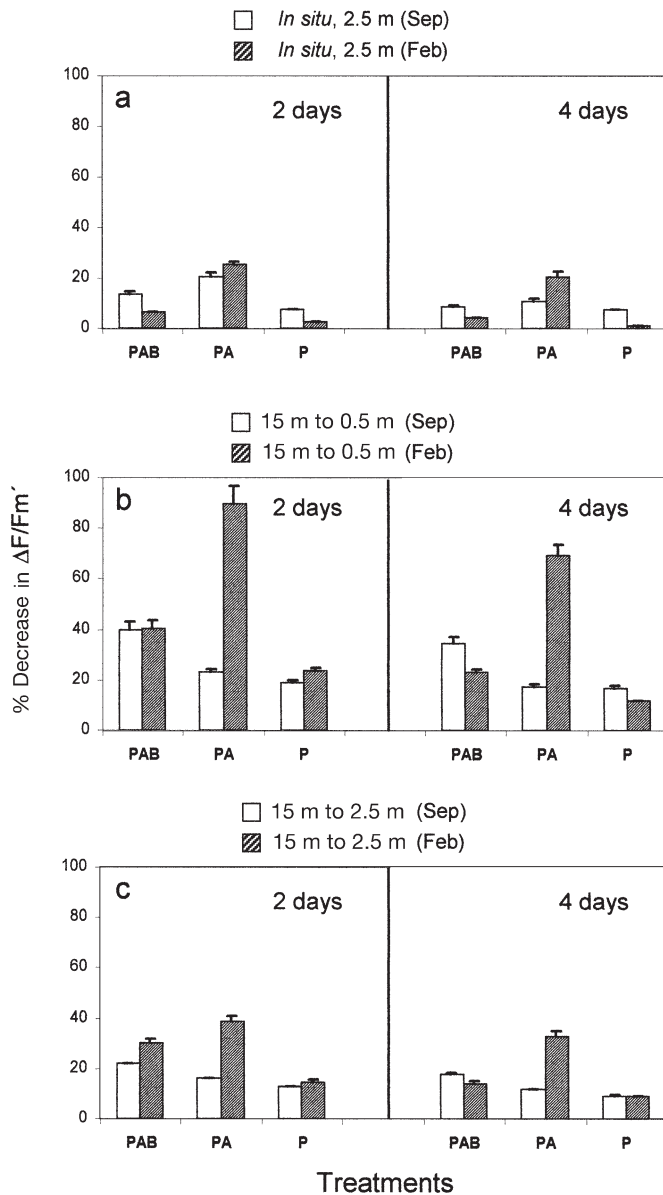
Fig. 4. *Posidonia oceanica.* Percentage decrease in $\Delta F/F_{m}'$ at noon in (a) plants at their natural growth site (2.5 m depth), and shoots transferred from (b) 15 to 0.5 and (c) 2.5 m depth. The seagrass was exposed for 2 and 4 d to full solar irradiance (PAB), solar irradiance without UV-B (PA) and solar irradiance without UVR (P)

noon in both seasons. Thus, dynamic photoinhibition is expected at the natural site of growth of *P. oceanica*

ETR (calculated in this case using the values of incident solar irradiance at each season) was significantly higher (Tukey's test, p < 0.01) in summer than in winter, due to higher irradiation in September. In spite of the decrease in the effective quantum yield at noon, no parallel decay of ETR was observed at any season

during the noon hours (Fig. 3b). Maximal ETR and E_{k} (under LED light) were about 3 times higher in summer than in winter (Fig. 3c and Table 2). The photoinhibition irradiance in September was ~540 µmol m^{-2} s^{-1} and 220 µmol m^{-2} s^{-1} in February. ETR versus irradiance was also determined in plants incubated for 4 d at 2.5 m depth under P, PA and PAB (Table 2). Maximal ETR and E_{k} were significantly higher (Tukey's test, p < 0.05) in summer than in winter in all light treatments; moreover, the smallest values of ETR were found in the PA treatment in both seasons. Maximal ETR and E_{k} did not change significantly Tukey's test, (p > 0.05) after 4 d in PAB. However, after 4 d in PA, both ETR and E_{k} were significantly lower (p < 0.05) than initial values (Table 2). Maximal ETR was highest and E_{k} lowest in shoots pre-incubated under P compared to other light treatments in both seasons.

The decrease in $\Delta F/F_{m}'$ at noon in *Posidonia oceanica* growing at 2.5 m was significantly higher (Tukey's test, p < 0.05) under PA in both seasons (a drop of about 20% from morning values: Fig. 4a) than under the other light treatments. However, under P and PAB, the decrease was less than 20%, being more pronounced in September than in February (Fig. 4a). Under P, the decrease in $\Delta F/F_{m}'$ was significantly (Tukey's test, p < 0.05) higher in September than in February after both 2 and 4 d. However, under PAB, significant differences (Tukey's test, p < 0.05) among seasons were observed only after 2 d.

Table 2. *Posidonica oceanica.* Maximal electron transport rate (ETR$_{max}$) and saturation irradiance for ETR (E_{k}) determined in plants collected from their natural growth site (2.5 m depth = initial), and after 4 d incubation at the same depth under full solar irradiance (PAB), solar irradiance without UV-B (PA) and solar irradiance without UV-A and UV-B (P). Experiments were conducted in September 1996 and February 1997. Means (±SD) calculated from at least 4 replicates for each light treatment in independent samples. Means were compared by applying a Model I 2-way ANOVA and Tukey's HSD test. Same letters indicate no significant differences, different letters indicate significant differences at p < 0.05

Treatments	ETR$_{max}$	E_{k}
Initial		
September	147.3 ± 1.4[a]	419.7 ± 27.9[a]
February	28.8 ± 2.7[b]	80.5 ± 7.0[b]
4 d in PAB		
September	133.5 ± 10.5[a]	300.3 ± 28.5[a]
February	33.8 ± 3.5[b]	118.5 ± 14.7[b]
4 d in PA		
September	113.5 ± 8.9[c]	380.5 ± 23.0[c]
February	29.8 ± 3.7[d]	148.5 ± 10.5[d]
4 d in P		
September	225.6 ± 15.3[e]	285.3 ± 15.9[a]
February	58.31 ± 4.5[f]	105.5 ± 13.6[b,e]

The percentage decrease in $\Delta F/F_m'$ was significantly higher (Tukey's test, p < 0.05) in seagrasses transferred from 15 to 0.5 m (Fig. 4b) or to 2.5 m (Fig. 4c) than in plants incubated at 2.5 m (Fig. 4a). The decrease was significantly higher in plants transferred from 0.5 m (Tukey's test, p < 0.05) than in those growing at 2.5 m, and always more pronounced under PA than under P and PAB in February. However, in September, the decrease in $\Delta F/F_m'$ was significantly higher (Tukey's test, p < 0.05) in PAB than in PA or P in plants transferred from 0.5 or 2.5 m to 15 m. The lowest decrease was found in the P treatment, indicating that photosynthetic efficiency was affected by UV. Moreover, the negative effects of UV-A radiation were more pronounced in the absence of UV-B. Thus, UV-B seemed to be necessary to partially ameliorate the photoinhibitory effect of UV-A. In the PA treatment, the decrease was significantly more pronounced (Tukey's test, p < 0.05) in February than in September, while no significant seasonal differences appeared in the P and PAB treatments. The percentage decrease in $\Delta F/F_m'$ in shoots transferred from 15 to 0.5 m was significantly higher (p < 0.05) under PAB than under P after both 2 and 4 d and in both seasons. In February, the decrease in $\Delta F/F_m'$ under PA or P was significantly higher (Tukey's test, p < 0.05) after 2 d than that after 4 d; however, this was not the case in September. The absence of UV-B radiation seemed to have more quantitative effects in winter than in summer. The reduction in the decrease in $\Delta F/F_m'$ with time in plants transferred from 15 to 0.5 and 2.5 m (lower inhibition after 4 d at the new depth: Fig. 4b,c), might indicate partial acclimation to high irradiance in transferred plants.

Recovery of the $\Delta F/F_m'$ decrease was significantly (Tukey's test, p < 0.05) lower in plants transferred from 15 m than in those living at 2.5 m depth (Fig. 5). Seagrasses collected at 2.5 m depth showed a higher capacity for recovery than those transferred from 15 to 0.5 or to 2.5 m. At 2.5 m, recovery was significantly higher (Tukey's test, p < 0.05) in February than in September after 4 d. In plants growing at 2.5 m, the recovery in the afternoon was similar, close to 100%, independent of light treatment and season. In plants transferred from 15 to 0.5 m in September, recovery was significantly higher (Tukey's test, p < 0.05) in PA and P than in PAB after both 2 and 4 d. Recovery was higher (Tukey's test, p < 0.05) in September than in February under PA after both 2 and 4 d. Under P, significant differences (Tukey's test, p < 0.05) in September compared to February were found only after 4 d. In plants transplanted from 15 m to 2.5 m, after 2 d, recovery was significantly higher (Tukey's test, p < 0.05) under PA and P than under PAB; however after 4 d no significant differences among treatments were found. Thus, in transferred plants, recovery increased

when the incubation period was extended to 4 d, indicating acclimation to high irradiance (Fig. 5b,c).

Decrease and recovery of $\Delta F/F_m'$ after short-term (30 min) exposure to solar irradiance

As part of the inhibition/recovery experiments, leaves of *Posidonia oceanica* were exposed for 30 min to solar irradiance at the water surface. A significant decrease in $\Delta F/F_m'$ (Tukey's test, p < 0.05) in *P. oceanica* collected from 2.5 m was observed after 30 min exposure at the water surface at noon (Fig. 6). The decrease was significantly higher (Tukey's test, p < 0.05) in February than in September, although solar irradiance during exposure was higher in September
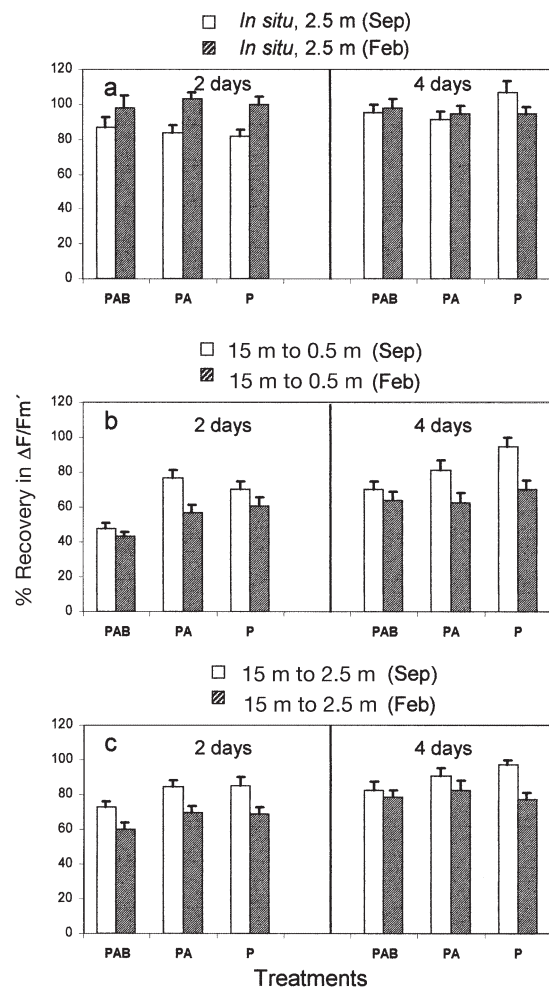

Fig. 5. *Posidonia oceanica.* Percentage recovery in $\Delta F/F_m'$ in the afternoon in (a) shoots collected at their natural growth site (2.5 m depth), and shoots transferred from (b) 15 to 0.5 and (c) 2.5 m depth. The seagrasses were exposed for 2 and 4 d to full solar irradiance (PAB), solar irradiance without UV-B (PA) and solar irradiance without UVR (P)
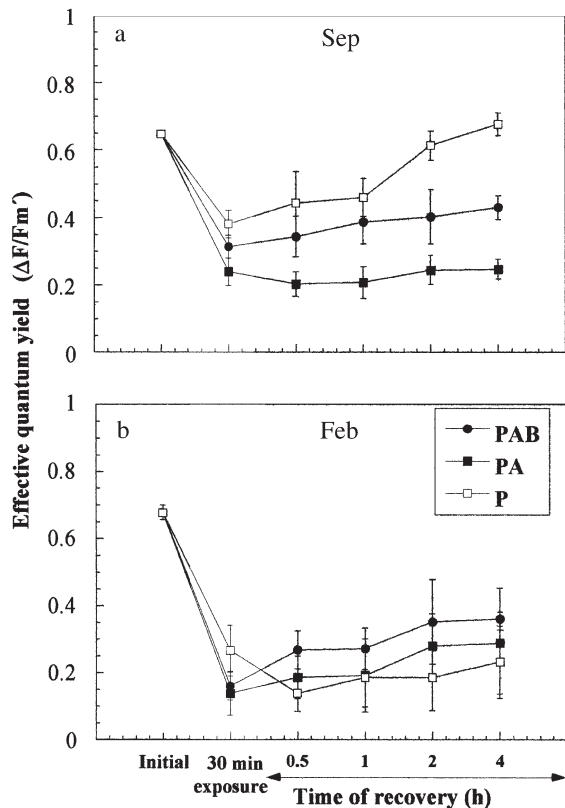
Fig. 6. *Posidonia oceanica*. Effective quantum yield ($\Delta F/F_m'$) of plants from 2.5 m depth exposed to a short-term (30 min) high irradiance treatment (exposure in surface waters at noon time) and during recovery (exposure to unfiltered solar irradiance in the shade at ca. 50 µmol m^{-2} s^{-1}). The experiments were conducted in (a) September 1996 and (b) February 1997. During the high-irradiance treatments, shoots were exposed to PAB, PA and P

than in February. At noon, PAR irradiance was 450 and 307 W m^{-2}, UV-A was 42 and 29 W m^{-2}, and UV-B was 2.0 and 1.2 W m^{-2} in September and February respectively.

After 30 min exposure, recovery of $\Delta F/F_m'$ was computed during the next 4 h, with the plants exposed to low solar irradiance. Recovery was completed only in the P treatment in September (Fig. 6a). In February, recovery was very low in all the cases (29 to 51% of the initial values, depending on light treatment). In September, recovery of $\Delta F/F_m'$ was significantly higher (Tukey's test, p < 0.05) under P and PAB than under PA. However, in February, the recovery was similar under all light treatments (Fig. 6b). Thus, short exposure to high irradiance promoted a significant decrease in $\Delta F/F_m'$, with almost no recovery. This result differed from that for *Posidonia oceanica* at its natural growth site at 2.5 m (Figs. 4a & 5a) where full recovery occurred.

In order to investigate the effects of the absence of UV on $\Delta F/F_m'$, plants previously incubated for 4 d at 2.5 m under P, PA and PAB were submitted to short-term exposure (30 min) of high solar irradiance (at the water surface) of P, PA and PAB (Fig. 7). Highest photoinhibition was produced in P-pretreated plants. After preincubation for 4 d under PAB (Fig. 7 a), the decrease in $\Delta F/F_m'$ was significantly higher (Tukey's test, p < 0.05) after short-term exposure (30 min) in PAB than that under PA and P; the decrease in $\Delta F/F_m'$ was significantly higher (Tukey's test, p < 0.05) in February than in September under only PA and P exposure.

After preincubation for 4 d in PA significant differences between February and September (Tukey's test, p < 0.05) were only found under short-term exposure in P. The decrease in $\Delta F/F_m'$ was significantly higher (Tukey's test, p < 0.05) after short exposure to PAB than to PA and P. Finally, after preincubation for 4 d under P no significant differences among the light treatments
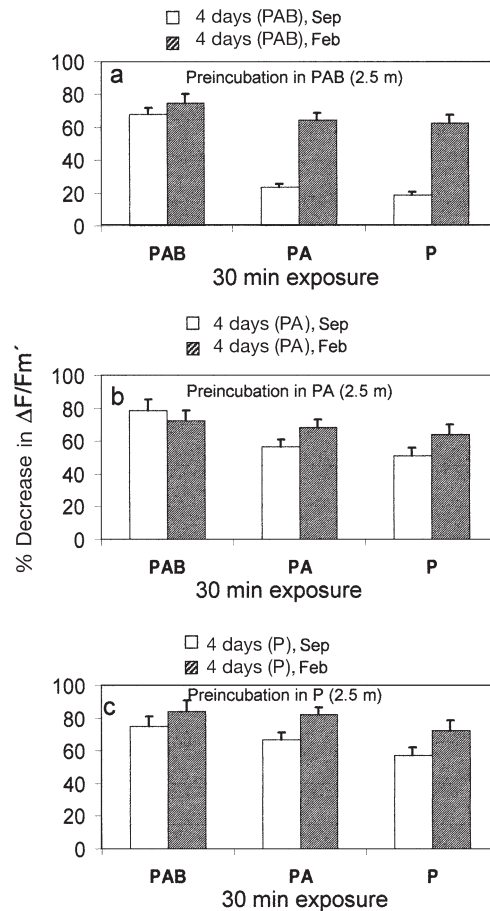

Fig. 7. *Posidonia oceanica*. Percentage decrease in $\Delta F/F_m'$ after 30 min exposure to high solar irradiance in PAB, PA and P treatments. Shoots were previously acclimated for 4 d at 2.5 m to PAB, PA and P

were observed within either month. Significant differences ($p < 0.05$) between February and September were found for short-term exposure under PA and P but not under PAB.

DISCUSSION

Posidonia oceanica seems to be well acclimated to the high irradiance conditions of Cabo de Gata (southern Spain), since it shows a relatively low decrease in effective quantum yield at noon and full recovery in the afternoon in plants incubated *in situ*. The decrease in $\Delta F/F_m'$ was higher in September than in February, since both solar radiation and transparency of the water column were higher in September than in February. Plants transferred from 15 to 2.5 m showed a higher decrease than those from 2.5 m, indicating a partial loss of photoprotective mechanisms in *P. oceanica* from deeper waters. Similar results have been reported by Ralph et al. (1998), who found that several seagrasses (including *P. oceanica*) from shallow waters had a higher capacity for non-photochemical quenching (e.g. protection from excessive radiant energy) than seagrasses from deeper waters. Also, Dennison & Alberte (1986) found lower photosynthetic rates when transplanting *Zostera marina* plants from 7 and 10 m depth to shallow waters. The photoprotective mechanisms seem to be rapidly stimulated, since inhibition decreased and recovery increased when the period after transference was extended from 2 to 4 d. Öquist et al. (1992a) suggested that there are mechanistic differences in the photoinhibition of sun and shade plants. Specifically, they proposed that sun plants can rapidly replace photoinhibited PSII reaction centres with photochemically active ones by means of an active repair cycle. In shade plants, however, this cycle would be less developed, with the PSII reaction centres that become inhibited providing protection to the remaining active centres by non-photochemical dissipation of excess excitation energy. This rapid acclimation to high irradiance conditions represents a strategy for survival in waters that are highly transparent to UV. In Cabo de Gata, 1 % of incident UV-B radiation penetrated to 11 m in February and to 22 m in September. Even though UV-B accounts for only a very small fraction of solar irradiance, it has been shown to have a considerable effect on the photosynthesis of macroalgae, inducing a significant decrease on their photosynthetic O_2 production (see Franklin & Forster 1997, Häder & Figueroa 1997).

There is limited information concerning the effects of UV radiation on marine angiosperms. Trocine et al. (1981) studied UV tolerance and photorepair capabilities of 3 species, and noted that *Halodule wrightii* had a high photosynthetic tolerance to UV-B, whereas *Syringodium filiforme* and *Halophila engalmanni* were more sensitive. It was speculated that all 3 species relied on epiphytic shading to reduce the degree of exposure to UV (Trocine et al. 1981). Dawson & Dennison (1996) showed different degrees of photoinhibition in several seagrasses in response to increased (+25 %) PAR and UVR. *Halophila ovalis* and *Halodule uninervis* were the most sensitive species, exhibiting the largest decrease in photosynthetic efficiency and chloroplast density. In the present study, we found different effects in *Posidonia oceanica* to those observed in macroalgae (Häder & Figueroa 1997). The presence of UV-A in the absence of UV-B (PA treatment) induced the highest degree of photoinhibition in *P. oceanica* (Fig. 4). Also, UVR might be involved in the stimulation of photoprotection mechanisms, since short-term exposure to high solar irradiance induced higher photoinhibition in plants preincubated (4 d) under P than those preincubated under PA or PAB (Figs. 5 & 7). These results contrast with those reported for most macroalgae, in which the largest photoinhibition occurred under full solar irradiance (Wood 1987, Häder et al. 1996, 1997). However, recently, a beneficial role of UV-B radiation in the repair process of photosynthesis has also been suggested (Flores-Moya et al. 1999). In *P. oceanica*, photoprotection mechanisms could also be stimulated by UV-radiation. In addition, some enzymatic activities (e.g. nitrate reductase and carbonic anhydrase) are also stimulated by UV-A or UV-B radiation in several macroalgae (Flores-Moya et al. 1998, Gómez et al. 1998) and in *P. oceanica* (Viñegla 2000).

The photoprotection mechanisms of *Posidonia oceanica* are still unknown, but according to our results the presence of UV-B seems to diminish the degree of photoinhibition at noon. However, UV-B seems not to be essential to recovery, since this was higher under PA than under PAB. The photoinhibition and recovery processes would therefore seem to be differently photoregulated. Daily dynamic photoinhibition (Osmond 1994), including an increase of non-photochemical quenching at noon (data not shown), can constitute, per se, a photoprotection mechanism. Öquist et al. (1992b) indicated that photoinhibition of photosynthesis represents a mechanism for long-term regulation of the PSII. Structural changes in the D1 protein facilitates the formation of a population of dissipative PSII centres that do not participate in linear electron transport to PSI (Critchley & Rusell 1994). Dynamic photoinhibition following a diurnal pattern has been found in several macroalgae (Henley et al. 1991, Figueroa et al. 1997, Häder et al. 1996, 1997): the algae were photoinhibited by excess light at noon, followed by recovery in the afternoon of effective quantum yield and photosynthesis. High solar irradiance reduces the photosyn-

thetic activity of marine algae (Hanelt et al. 1994, Häder et al. 1996, 1997, Hanelt 1996), as demonstrated by a decrease in the effective quantum yield and photosynthetic O_2 production. As reported for macroalgae (Häder & Figueroa 1997), plants growing at the surface are much more resistant to photoinhibition than are deep-water species. Hanelt et al. (1993) and Häder & Schäfer (1994) found no significant recovery of photosynthesis in red algae exposed to full solar irradiance, indicating permanent photodamage rather than photoinhibition.

Another possible mechanism for protection is the accumulation of UV-absorbing substances. Prevention of UV damage by screening substances has been reported for several marine and terrestrial autotrophic organisms (Dunlap & Chalker 1986, Büdel et al. 1997, Karsten et al. 1998). Among these, mycosporine-like aminoacids (MAAs) have been recognised as performing an active photoprotective role. In *Posidonia oceanica*, a very high content of other UV-absorbing substances has been detected (e.g. polyphenolic compounds: Abdala & Figueroa unpubl. data), which play a possible photoprotective role against UV radiation. Trocine et al. (1981) suggested that the presence of flavonoids may reduce the degree of UV-induced inhibition in marine angiosperms, but they presented no data on the concentration of such UV-absorbing substances. Dawson & Dennison (1996) found that several seagrasses with a high tolerance to UVR (e.g. *Zostera capricorni*, *Cymodocea serrulata* and *Syringodium isoetifolim*) greatly increased the production of UV-blocking pigments in response to UV radiation.

In *Posidonia oceanica* the capacity for acclimation to high solar irradiance is clearly higher in summer than in winter. This was demonstrated by the different experiments carried out in this study: (1) In general, there was a higher decrease in $\Delta F/F_m'$ and a higher recovery in September than in February in both *Posidonia oceanica* from 2.5 m and in shoots transferred from 15 to 0.5 and 2.5 m (Figs. 4 & 5). (2) There was a lower decrease in $\Delta F/F_m'$ after short-term exposure (30 min in surface waters) to high solar irradiance and higher recovery (after 4 h under low irradiance) in September than in February (Fig. 6). (3) There was a higher maximal ETR and higher E_k in September than in February (Fig. 3 & Table 2).

In addition to light, temperature is another environmental factor that can affect photosynthetic rate and photoinhibition (Logan et al. 1999). Whereas the photophysical events of light-capture and charge separation are not strongly influenced by cold temperatures, Q_{10} effects upon enzymes of the Calvin cycle limit photosynthetic rates (Leegod 1995). Low temperatures can induce a decrease in the optimal quantum yield through an accumulation of photochemically inactive

reaction centres of the PSII (Krause 1994). Increasing temperature stimulates respiration and the repair process (resynthesis of the D1 protein) (Krause 1994). Ekelund (2000) discussed the importance of respiration in the repair mechanisms of photoinhibition for phytoplankton. The differences between the electron transport rates in summer and winter could be also due to temperature. However, in Cabo de Gata waters, differences between winter and summer temperatures are not very high (only 6 ± 1°C) and no drastic temperature effects on photosynthesis, as reported for plants of colder systems (Krause 1994, Logan et al. 1999) would be expected. A sufficiently high ambient temperature may be necessary for high activity of the dark reactions, so that the marine macrophytes do not suffer from light stress on a sunny day in the Mediterranean zone. If most of the absorbed energy can be used for photochemical reactions, photosynthesis is not severely stressed by light and, hence, photoinhibition of PSII would not occur.

In this work, we have shown that the response to high UVR in *Posidonia oceanica* differs from that of other marine macrophytes in southern Spain (Figueroa et al. 1997, Häder & Figueroa 1997, Figueroa 1998, Flores-Moya et al. 1998, Häder et al. 1998). In general, in most macroalgae that have been analysed, PAB induces higher photoinhibition than PA or P. In contrast, in *P. oceanica*, the relatively rapid alteration in its tolerance to high irradiance, e.g. preincubation under PAR for 4 d or exposure to only PAR + UV-A, indicates that the presence of UV-B is necessary for maintaining or stimulating photorepair mechanisms. Thus, the high levels of UV-B during the summer may activate these dynamic photoinhibition mechanisms, since the radiation is high enough to reach young leaves that are not directly exposed. The availability of UV-B is a result of very clear waters. This indicates that UVR and high PAR in the field could act as triggers for the induction of photoprotective mechanisms against UV radiation. Hanelt et al. (1997) showed that polar macroalgae cultivated for a long period in the laboratory retained certain genetic adaptations to the natural environment. In *P. oceanica*, light environmental signals (trigger elements) seem also to be necessary to stimulate photoprotective mechanisms during photoinhibition and recovery. One of these possible signals could be the ratio UVR/PAR. Smith et al. (1992) indicated that changes in the UVR/PAR of natural radiation better explained photoinhibition induced by solar irradiance than the absolute amount of PAR or UVR. The ratio UVR/PAR could act as an environmental signal, and both photoinhibition and photoprotection mechanisms could be modulated by variations in this ratio. These variations have been shown to occur through the day and throughout the year, and to be altered by the

presence of clouds (Madronich 1993, Gautier et al. 1994). As an analogy, it is known that in both terrestrial plants (Smith 1993) and algae (Rüdiger & López-Figueroa 1992, Figueroa 1996) the environmental variation in another light ratio (e.g. red:far-red) acts as an environmental signal. The ratio among different light broadbands is dependent on the level of radiation, which is variable over the year. Thus, the absence of an environmental signal in winter and autumn may be due to the low irradiance during these seasons, while in summer UV-B levels are sufficiently high to activate photoprotection mechanisms that are present, but not active, in winter.

In conclusion, our results suggest that the presence of UVR is necessary for the activation of photoprotection mechanisms in marine seagrasses; however, more research is necessary to discover the exact roles of UVR and of the UVR:PAR ratio as environmental signals.

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